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Aberrant Leaves on Angle-Shoots of Selaginella martensii Spring[1]

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Dorsal and ventral angle-meristems, which normally develop into roots (Webster and Steeves, 1967), are present at most points of shoot branching in the heterophyllous species *Selaginella martensii* Spring. But in stem segments that are surgically isolated from the intact plant and which are incubated on moist filter paper, these angle-meristems may develop as angle-shoots (Williams, 1937; Webster, 1969) (*Fig. 6*). In a recent study of angle-meristem development in excised stem segments of *S. martensii* (Webster, 1969), most leaves (microphylls) on angle-shoots were normal, according to the description by Harvey-Gibson (1897). But some, particularly those near the base of angle-shoots, were abnormal. The morphology and possible significance of these aberrant leaves is presented in this paper.

Normally, the larger, ventral leaves of the angle-shoots are lanceolate, with a narrow, bluntly pointed apex (*Fig. 1*). The smaller, dorsal ones are ovoid oblique and end in a long, stiff awn (*Fig. 2*).

Both dorsal and ventral leaves possess marginal teeth and are asymmetrical at the base. A single median vascular strand is present, and a ligule occurs at the leaf base on the adaxial surface. Conspicuous rows of stomata occur along the vascular strand (*Fig. 7*).

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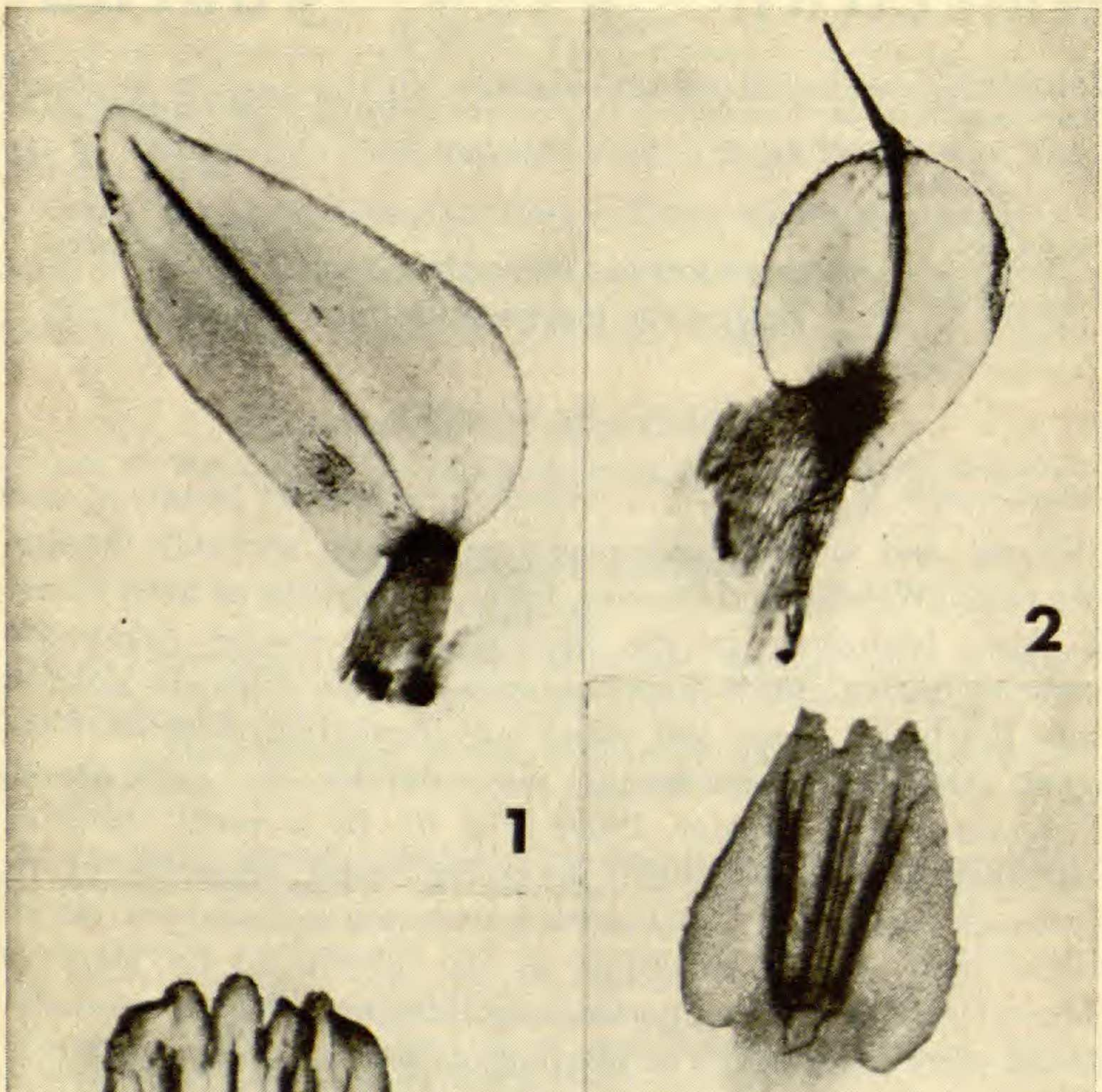


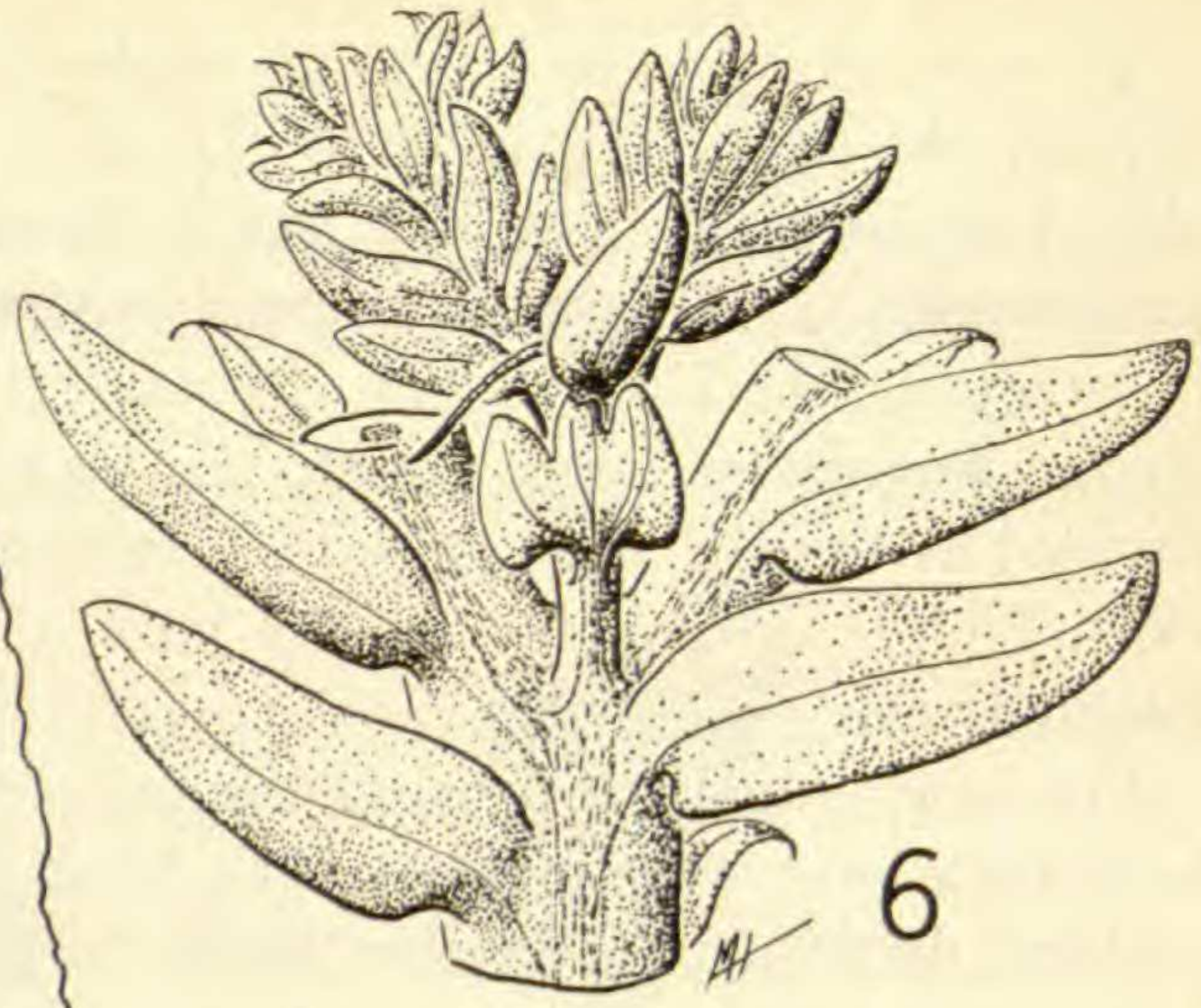
Cleared and Stained Leaves of Selaginella martensii
Angle-shoots Showing Vascular Strands

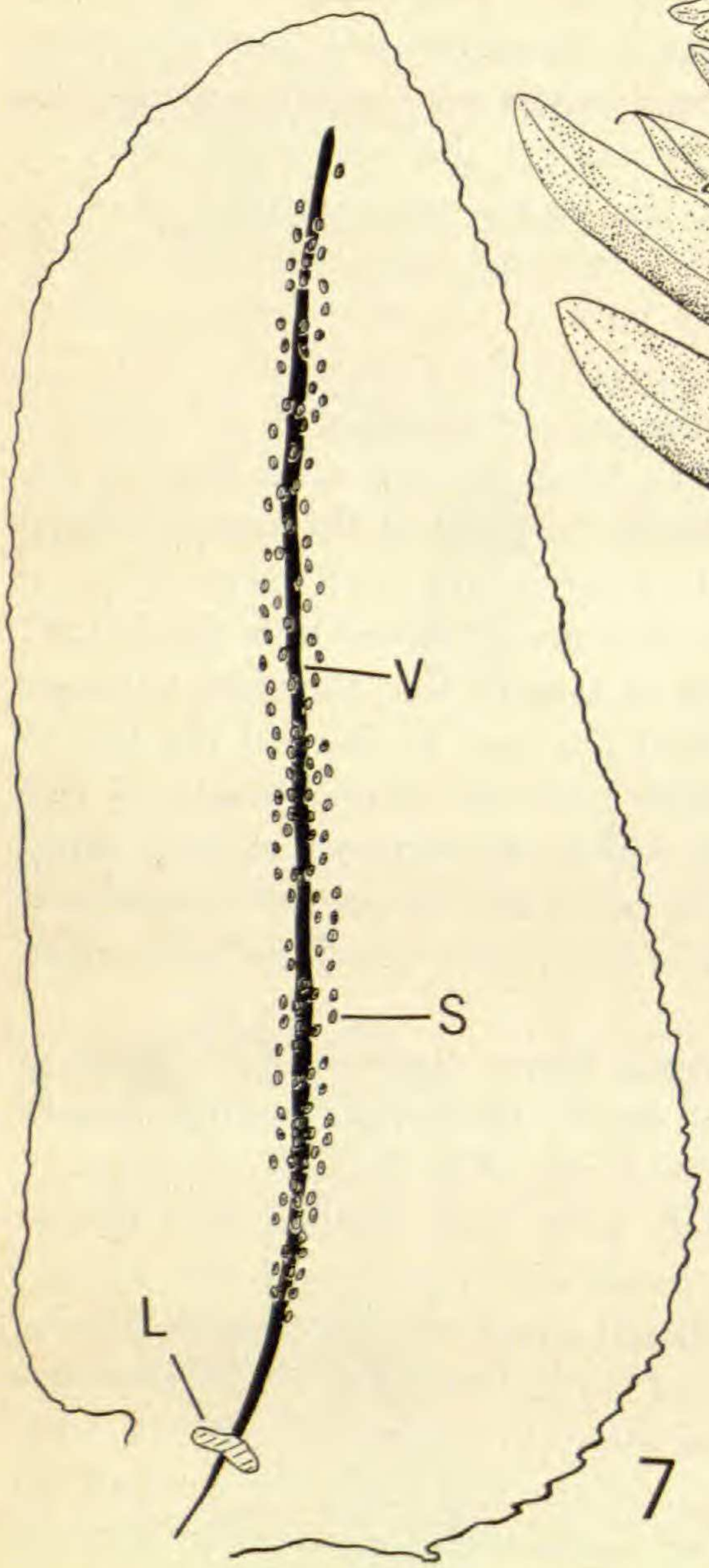
In contrast to most leaves on angle-shoots, the first few leaves toward the base, proximal to the first branching of the angle-shoot, are aberrant (*Figs. 3*, *4*, and *6*). In addition to these abnormal basal leaves, a few cases of unusual leaves were found more distally on angle-shoots. Both dorsal and ventral aberrant leaves vary in shape. Instead of being entire, the leaves are variously lobed or divided at the tip (*Figs. 3* and *4*). In some cases they are deeply cleft. Unlike normal leaves, the base of aberrant leaves is often symmetrical.

For anatomical study, angle-shoots were cleared in 2% sodium hydroxide and were stained with basic fuchsin according to the method described by Jacobs (1952). Instead of the normal single vascular strand, several strands occur in aberrant leaves (*Figs. 3* and *4*). As many as seven strands were observed in a single leaf. In most leaves one strand could be traced from the stem vascular system toward the leaf base. Near the base of the leaf the strand is divided, usually dichotomously, one to several times. A few ventral leaves were observed in which two separate strands could be traced from the stem into the leaf base. In neither normal nor aberrant leaves is the departure of leaf traces associated with a gap in the stem vascular cylinder.

In normal and in most aberrant leaves the vascular system is closely associated with a single ligule. However, in some deeply cleft leaves, two separate ligules occur (*Fig. 5*) and one or more vascular strands are associated with each ligule. Ball (1925) reported sporophylls of *S. martensii* which possessed two ligules, one of normal size and an additional smaller ligule. Double ligules found in the present study were of normal size (*Fig. 5*). In aberrant leaves each vascular strand has stomata associated with it, and, compared to normal leaves, more of the leaf surface is covered by stomata (*Figs. 7* and *8*). The arrangement of stomata in distinct rows is not so evident as in normal leaves.

FIG. 1. NORMAL VENTRAL LEAF, × 23. FIG. 2. NORMAL DORSAL LEAF, × 22. FIG. 3. ABERRANT VENTRAL LEAF, × 46. FIG. 4. ABERRANT DORSAL LEAF, × 42. FIG. 5. ABERRANT DORSAL LEAF WITH TWO LIGULES. SOME STEM TISSUE VISIBLE THROUGH LEAF, × 47.





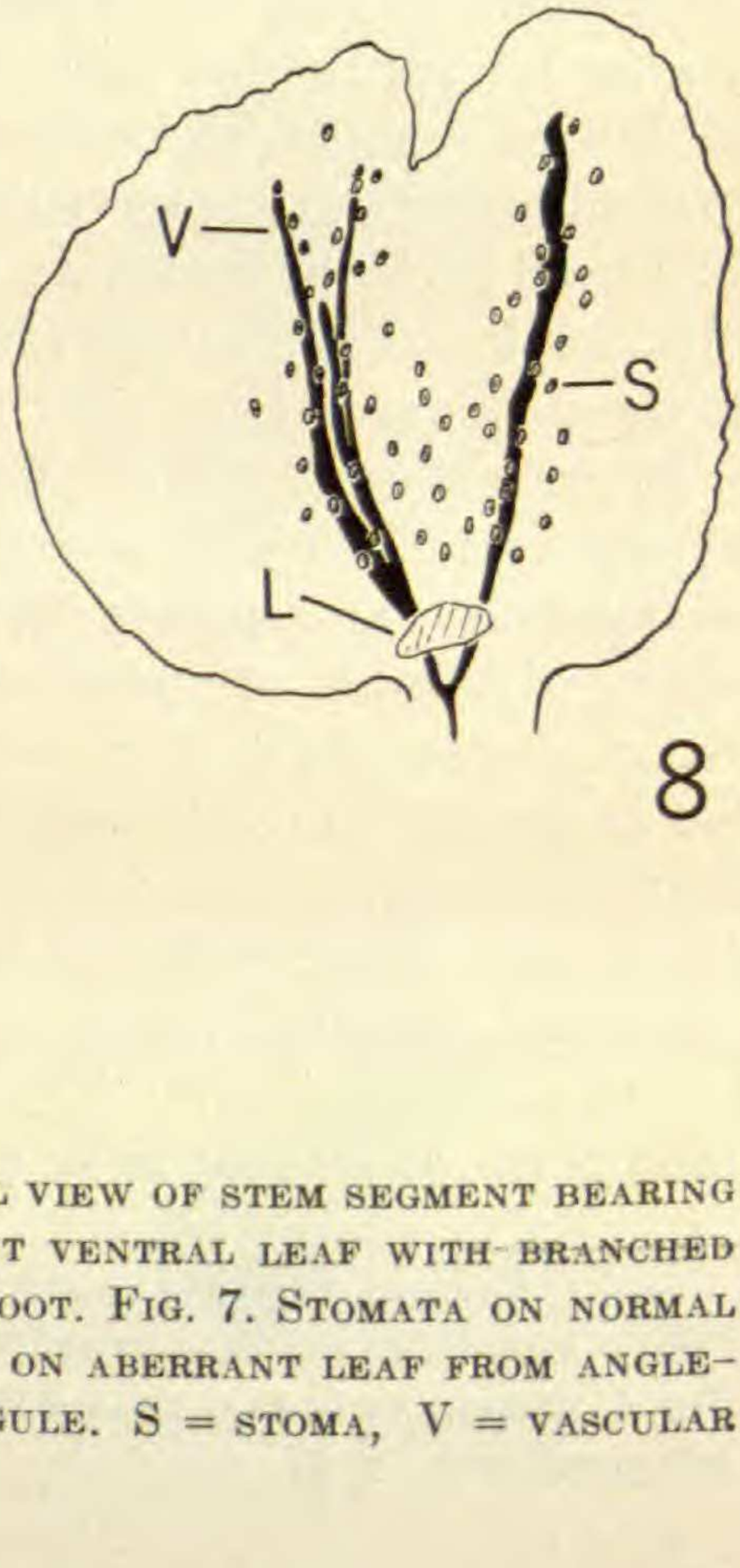


PLATE 2. FIG. 6. DIAGRAM OF VENTRAL VIEW OF STEM SEGMENT BEARING AN ANGLE–SHOOT. NOTE SINGLE ABERRANT VENTRAL LEAF WITH BRANCHED VASCULATURE TOWARD BASE OF ANGLE-SHOOT. FIG. 7. STOMATA ON NORMAL LEAF FROM MAIN SHOOT. FIG. 8. STOMATA ON ABERRANT LEAF FROM ANGLE–SHOOT. The abbreviations are: L = LIGULE. S = STOMA, V = VASCULAR STRAND.

DISCUSSION

Grambast and Rosello (1965) described leaves of *S. willdenovii* (Desv.) Baker in which there were two or three veins from the dichotomous branching of a single vascular trace. According to their illustrations, the leaves themselves were not so distinctly lobed or divided as the aberrant leaves described here in *S. martensii*. The authors made no mention of stomata or ligules in the leaves of *S. willdenovii*, but they did discuss possible phylogenetic implications of the branched vasculature. They cited fossil lycopods (*Protolepidodendron* Krejci, *Duisbergia* Kräus. and Weyl., and *Sigillaria scutellata* Brongn.) which possessed leaves with dichotomously branched vascular strands, and suggested that in *S. willdenovii* microphylls with dichotomizing veins represent a primitive condition. According to their view, microphylls with a single vein could have been derived by reduction. They suggested that, like megaphylls, microphylls may, in some cases, have been derived from a system of axes.

One could apply a similar interpretation to the microphylls of *S. martensii*. Aberrant leaves with branched vasculature could be interpreted as representing a primitive condition, and normal leaves with a single vascular strand a more advanced condition. A comparison of normal and aberrant leaves would suggest that during evolution lobing, number of vascular strands, and rows of stomata were reduced.

According to the theory of recapitulation (ontogeny, in abbreviated fashion, repeats phylogeny), the position of leaves on angle-shoots could be used to indicate a primitive or an advanced condition. Although usually applied to progressive development from juvenile to adult leaves in sporelings or seedlings, Takhtajan (1959, p. 91) has applied this theory to leaves occurring on accessory shoots. Angle-shoots would fit into this latter category. According to the theory, the progression of microphylls in angle-shoots represents at least some stages in the evolution of microphylls for *S. martensii*. Thus aberrant leaves occurring at the base of angle-shoots would represent a primitive condition, and more distal (normal) leaves an advanced condition (*Fig. 6*). However,

as Foster and Gifford (1959, p. 9) have stated, whether juvenile leaves provide reliable evidence to the morphology of ancestral leaf types is questionable, and hypotheses based on the theory of recapitulation should always be made with great caution. It should also be noted that the features found in aberrant leaves of *S. martensii* are not known in fossil representatives of *Selaginella* or in *Selaginellites*. At the present time there is no strong evidence to indicate that aberrant microphylls in *Selaginella* do in fact represent a primitive condition. Rather than having any phylogenetic significance, the aberrant leaves in *S. martensii* merely may be the result of abnormal development during the early ontogeny of angle-shoots.

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